

Host Discrimination by the Gregarious Parasitoid *Oncophanes americanus* (Hymenoptera: Braconidae)

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Abstract.—Tests of host discrimination by the external, gregarious parasitoid *Oncophanes americanus* Weed demonstrated that host size plays a significant role in determining both the number of eggs oviposited and the sex ratio of the parasitoid progeny. Number of larvae developing per host averaged 1.4, 3.1, and 8.2 for 3rd-, 4th-, and 5th-instar hosts, respectively. A high percentage of 2nd- and 3rd-instar hosts were stung without oviposition. The percentage of female adult parasitoids emerging from hosts increased from 62% for 3rd instars to 81% for 5th instars. Superparasitism was defined in terms of the efficiency of host resource conversion (ERC) by the parasitoid larval cohort. ERC is equal to the ratio of the biomass of the mature larval brood to the initial host biomass available for consumption. For *O. americanus* parasitizing larvae of the leafroller *Argyrotaenia citrana* (Fernald), significant increases in mortality of parasitoid larvae occurred at values of $ERC > 0.6$.

Host discrimination by hymenopteran parasitoids can be defined as the behavioral capacity to avoid superparasitism or multiple parasitism. Early reviews of this topic restricted their definition of host discrimination to the ability of a parasitoid to distinguish unparasitized from parasitized hosts (Vinson, 1976; Lenteren, 1981). This definition appears biased towards solitary species and does not adequately explain the discriminatory behavior of gregarious parasitoids. In addition, to avoiding oviposition in parasitized hosts many gregarious species are able to discriminate the size of their host and regulate the number of eggs deposited (Klomp and Teerink, 1962; Purrington and Uleman, 1972).

The nature of superparasitism by gregarious species differs in a number of ways from solitary species. First, the occurrence of superparasitism is dependent upon the relative size of the host and size and number of developing parasitized larvae. Therefore, egg frequency distributions on hosts cannot be used to detect superparasitism. Secondly, competition by gregarious individuals on a host generally does not involve physical combat or physiological suppression. Instead, larval mortality is primarily due to starvation and sexual differences in survivorship may create pronounced alterations in the progeny's sex ratio (Chacko, 1964; Wylie, 1966). In addition to higher mortality, indirect effects such as decreased adult size, longevity, and fecundity commonly result from superparasitism.

More recent studies of host discrimination and superparasitism in gregarious species have investigated the role of natural selection on parasitoid reproductive strategy (Hassell et al., 1983; Waage and Ming, 1984). These studies have provided a theoretical treatment of optimal sex ratio and clutch size which maximize adult

fitness (Charnov and Skinner, 1984). Yet these studies still do not adequately quantify the relation between available host resources and parasitoid larvae utilization which determine superparasitism for gregarious species.

In this paper, we report data on the ability of the gregarious ecto-parasitoid *Oncophanes americanus* Weed to exercise host size discrimination as measured by the relation between host size and number of eggs deposited and the sex ratio of its progeny. In addition, we propose a definition of superparasitism based on the efficiency of resource (host) biomass conversion by the parasitoid.

MATERIALS AND METHODS

Adult *O. americanus* were maintained in 1.7-liter screened cardboard containers and supplied with honey and water. The adult sex ratio of the colony was approximately 10:1 female:male. The parasitoids were reared on larvae of the leafroller *Argyrotaenia citrana* (Fernald) which is a common host for *O. americanus* in caneberry, *Rubus* spp. in the Pacific Northwest (Coop, 1982). Host larvae were reared on a synthetic codling moth diet (BioServe, Frenchtown, NJ). Pupae were transferred to screened emergence containers where adults oviposited on folded wax paper strips. Eggs were harvested, rinsed in a 1% chlorox solution and hatched in a glass bell jar. Both parasitoid and host colonies were reared at $25 \pm 1^\circ\text{C}$ with a 16:8 (L:D) photoperiod.

Individual host larvae were exposed to a single, mated *O. americanus* female (10–15 days old) in 28-ml plastic cups for 3 days. Initial stinging and beginning of oviposition occurred within 12–24 hr. The complete batch of eggs oviposited on any one host were generally laid within 12–36 hr. *O. americanus* eggs hatch within 24 hr and it was rarely observed that a parasitoid laid a second batch of eggs on its host during the experiment. Honey was provided in the cup for the parasitoid and a small block of artificial diet was provided as food and a refuge for the host. Prior to all experiments, host larvae were weighed and their head-capsules measured to determine their age class (Coop, 1982).

To avoid disturbing the host and attached parasitoid eggs, counts of parasitoids per host were based on young larvae. If no larvae were observed after 2 days, hosts were carefully examined for eggs. In general, egg mortality was very low, ca. 1%.

Superparasitism by a gregarious parasitoid was defined in terms of biomass conversion of the host. The efficiency of host resource conversion (ERC) is defined as equal to $\text{PAR}/(\text{HOS} - \text{REM})$ where PAR equals the combined weight of the entire brood of mature parasitoid larvae developing on a single host and weighed as a group after leaving their host and before pupation; HOS equals the host weight at the time of parasitism; and REM equals the biomass of the host which is not available to the parasitoid (this includes the cuticle and other chitinized structures). Remains of 50 heavily utilized hosts were weighed to assess the fraction of host biomass not available to parasitoids. REM was determined to be a linear function of HOS. $\text{REM} = -0.214 + 0.133\text{HOS}$; $R^2 = 0.97$, $P < 0.001$.

RESULTS AND DISCUSSION

Adult female *O. americanus* attacked and paralyzed 2nd–5th-instar *A. citrana*, but seldom oviposited on hosts weighing < 2 mg, i.e., 2nd and early 3rd instars (Table 1). A significant linear relationship ($R^2 = 0.86$, $P < 0.05$) was found for

Table 1. Summary of parasitism of the host *Argyrotaenia citrana* by the gregarious ecto-parasitoid, *Oncophanes americanus*.

	Larval stadium			
	Second	Third	Fourth	Fifth
Hosts exposed	60	120	68	115
Hosts stung	0	23	39	71
Hosts stung with no eggs	35	50	18	13
Larvae in cohort	0	1.4 ± 0.33	3.1 ± 1.35	7.9 ± 3.61
Sex ratio F/M	—	1.8	2.7	3.3

host weight and number of eggs oviposited. The average number of eggs deposited per host leveled off on hosts larger than 30 mg.

The average weight (\pm SD) of a 2nd-instar host larva was 0.3 ± 0.15 mg, and a mature parasitoid larvae weighed 1.2 ± 0.38 mg. Obviously, a 2nd-instar host could not support the development of a single parasitoid. While over 50% of the 2nd-instar hosts exposed were stung and killed, no eggs were deposited.

Third-instar hosts averaged 2.2 ± 0.21 mg and could potentially support 1 or 2 parasitoid larvae. Females oviposited on over 20% of this host size class and brood size averaged 1.4 ± 0.30 eggs per host. The biomass of hosts with two parasitoid larvae was usually completely utilized before both larvae completed development, and survivorship of these parasitoids to the adult stage was low.

Weight gain by the 4th- and 5th-instar hosts is rapid with the weight of 4th- and 5th-instar hosts averaging 7.8 ± 1.3 mg and 28.2 ± 3.3 mg, respectively. Over 40% of all 4th instars exposed were stung with no eggs deposited. Successful oviposition on stung 4th-instar hosts reached 57% and brood size averaged 3.1 ± 1.3 eggs per host. Superparasitization of the host was rare in this size class. Nearly 20% of the hosts were stung with no eggs deposited.

Female parasitoids successfully oviposited on 62% of the 5th-instar hosts averaging 7.9 ± 3.6 eggs per host. Approximately, 20% of the hosts in this stage successfully pupated. Larvae about to pupate undergo morphological, as well as physiological, changes which appears to make them less suitable as hosts. *O. americanus* has not been reported to attack pupae (Coop, 1982).

Under our standardized laboratory conditions, the parasitoid response to host size was significant. However, several other factors may have an important impact in influencing the variability in the number of eggs deposited under field conditions. Obligate synovigenic species such as *Bracon hebetor* require a blood meal before their eggs can complete maturation (Benson, 1975). In contrast, *O. americanus* is able to mature eggs prior to host feeding. A comparison of egg deposition by 10 females on their first and second host revealed that the number of eggs increased significantly ($P < 0.05$) following host feeding (3.23–7.62 eggs per host). If hosts are not encountered over a period of time ovisorption of mature eggs can occur (Flanders, 1956). Dissections of 10 2-week-old females found 9.4 ± 4.7 eggs in their oviducts. Four-week-old females which had not been allowed to oviposit had 4.2 ± 1.7 eggs.

The number of host larvae stung without eggs deposited appears related to host size (Table 1). One explanation of the large number of 'empty' hosts may be that *O. americanus* avoids ovipositing on dead larvae. The dosage of venom injected

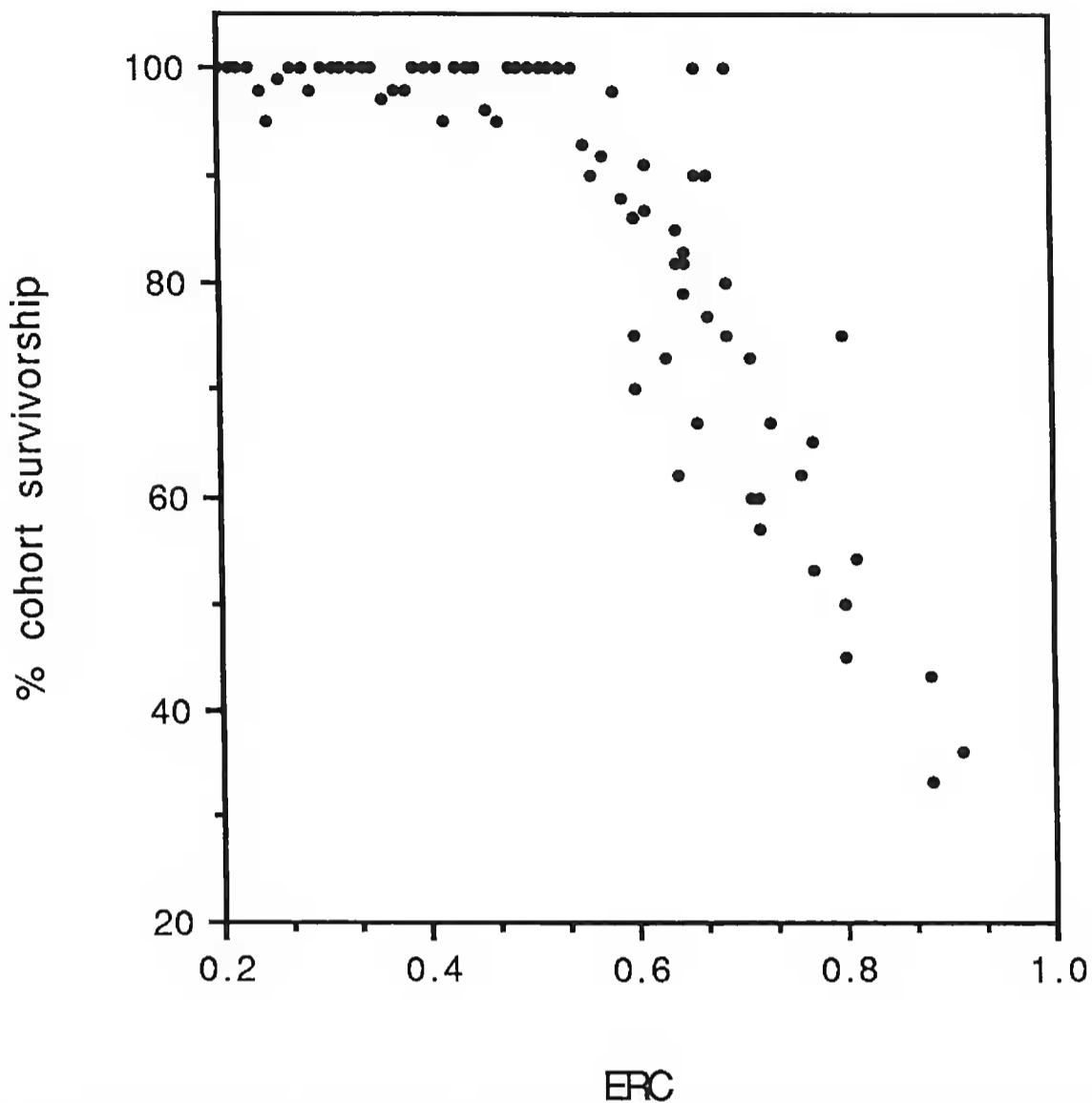


Figure 1. Percent larval survivorship of *Oncophanes americanus* in cohorts developing on the host *Argyrotaenia citrana* as a function of the host resource conversion index (ERC).

into smaller hosts can commonly cause premature death of the larvae (Beard, 1972). In comparison, larger larvae will remain alive after stinging for several days and can recover if isolated from the parasitoid. Another explanation may be that *O. americanus* has different thresholds for stinging and ovipositing. Host movement and attractant chemicals associated with silk production are specific cues responsible for initial stinging by *O. americanus* (ALK, unpubl. data). In comparison, oviposition is probably cued to the size of the host (Sandlan, 1979).

In haploid-diploid species, such as *O. americanus*, unfertilized eggs become males and fertilized eggs become females. Flanders (1965) suggested that for gregarious parasitoids, the sex ratio is likely modified by the ratio of oviposition and the secretory capacity of the spermathecal gland. The significant relationship between progeny sex ratio and host size ($R^2 = 0.91$, $P < 0.001$) in this study indicates that *O. americanus* actively regulates the production of fertilized eggs.

Plotting the index, ERC against the percent larval parasitoid survival showed that survival rates did not significantly decrease until ERC was greater than 0.6 (Fig. 1). Using this value to define superparasitism only 35 of the 350 host larvae exposed to *O. americanus* were superparasitized in our experiments. In comparison, the average value of ERC calculated for all 5th instars ($n = 115$) parasitized was 0.32 ± 0.15 in these experiments.

Superparasitism is known to affect the sex ratio of the surviving progeny (Wylie,

1966; Benson, 1975; Sandlan, 1979). Because male *O. americanus* larvae are smaller and develop more rapidly (0.8 ± 0.15 mg, 4.2 ± 0.35 days at 25°C) than female larvae (1.2 ± 0.22 mg, 4.9 ± 0.31 days at 25°C) competition for limited host resources would be expected to decrease female survivorship. In our experiments, the sex ratio from 15 superparasitized 5th instars ($\text{ERC} > 0.6$) was ca. 1:1 ($M = 74$, $F = 72$).

The results from this study suggest that host discrimination is probably an important factor affecting the population dynamics of *O. americanus*. Further study is needed to assess the occurrence of superparasitism in field populations. In addition, our study supports stronger recognition for the role of host size variability in studying parasitoid-host dynamics, especially temporal synchrony and interspecific competition within parasitoid guilds.

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